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ENDOSPERM IN THE FLOWERING PLANTS

by

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A Thesis Submitted for the Degree of

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Monotropa is described by Asa Gray(1) as destitute of chlorophyll and as growing parasitic on the roots of trees. He says there are two species, uniflora and hypopitys. Uniflora is waxy white, grows three to six inches high, and bears a single nodding flower of five petals and ten stamens. Hypopitys is downy, and tawny or more reddish in color, and grows from four to twelve inches high. It has several small flowers. The leaves of both species are so rudimentary as to be better described as scales.

Embryosac and Endosperm of Monotropa.

Strasburger(2) did his work on Monotropa hypopitys and prior to 1877. His sectioning was "free-hand" and his fixing and staining material was osmic acid applied to the specimens after they were mounted under the cover-glass in water or often a solution of sugar in water. He said that the transparency of Monotropa makes it valuable for study of the embryosac. The ovules are numerous and anatropous. The nucellus consists of a single layer of cells surrounding a very large cell the nucleus of which is the proembryosac nucleus. As the ovule de-

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(1) Gray's School and Field Book Of Botany.

(2) Dr. Edward Strasburger Bufruchtung und Zelltheilung, pp., 33 and 70; figures 105 to 140, plates three and four.

velops, the cells surrounding the proembryosac cell are compressed laterally and their cell-walls at their ends disappear. The resulting nucellar tissue has a homogeneous appearance.

At the same time that the nucellar cells are undergoing this change, the proembryosac nucleus divides. Immediately the daughter nucleus which is nearer the micropylar end of the ovule, divides thus producing three nuclei in the proembryosac cell. The last two nuclei formed, those nearer the micropylar end of the ovule, and a part of the protoplasm are now surrounded by cell walls and are thus cut off from the large body of the proembryosac cell. What is left of this cell is much the greater part. It contains the third of the three nuclei mentioned above and is called the embryosac.(1) As growth proceeds, these two micropylar cells are partly absorbed, and the remaining part forms a cap at the micropylar end of the embryosac. This cap is dark colored because it refracts the light strongly.

The nucleus of the embryosac now divides. The daughter nuclei so produced take positions, one at the chalazal and the other at the micropylar end of the embryosac. Each of these nuclei now divide and immediately their daughter nuclei divide;

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(1) Strasburger l.c., Fig. 103.

but in a plane at right angles to the next previous division. These divisions produce eight nuclei; four at either end of the embryosac. Three of the nuclei at the micropylar end are now cut off from the other parts of the embryosac by membranous cell walls, and so become cells in the embryosac. Two of these three cells nearer the micropylar end of the embryosac are the synergidae; the other is the egg cell. These three cells together are known as the eggapparatus. Three of the four cells at the chalazal end of the embryosac are also surrounded by cell walls and these are known as the antipodal cells. The fourth nucleus of the micropylar and chalazal groups are called polar nuclei.(1) Each of these polar nuclei now move toward the center of the embryosac, where they unite and form the endosperm, or embryosac nucleus.(2) Strasburger (3) says that he has never met with a reduction of the synergidae to one in Monotropa but sometimes it appears as though there were only one synergid present. This he thinks is due to the view secured of the embryosac; it being such that one synergid is behind the other.

At this point the egg-cell is ready for fertilization and, if it takes place as is represented by Strasburger (4) the endo-

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(1) Strasburger l.c., Fig. 117.

(2) " " " 118-122.

(3) " " " 121.

(4) " " " 125-129.

inal protoplasm and forms the embryosac. The daughter cell which is nearer the micropylar end of the ovule now divides into two cells. A little later these two cells become disorganized and their remains become pushed up into considerable smaller space and make a refractive cap at the micropylar end of the embryosac.(1)

The nucleus of the embryosac is either the third or fourth nucleus arising from the proembryosac nucleus; for Strasburger fails to give any account of one of the four nuclei which typically rises from the macrospore-mother-nucleus. This embryosac nucleus now divides and a cell wall begins to be formed between its daughter nuclei making two cells of the embryosac with the nuclei, one at each end of said sac. But before thin cell wall is well formed between the two nuclei, it disintegrates and a vacuole is formed between the said nuclei. After this these daughter nuclei divide as in Monotropa until there are four nuclei at either end of the embryosac.

The cells of the nucellus in Orchis often persist until there are two nuclei at each end of the embryosac; but at this point their nuclei and cell walls fade and the nucellus appears as a homogeneous tissue. As soon as the four nuclei are formed

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(1) Strasburger, l.c., Figs. 73-75.

at either end of the embryosac, the egg apparatus, the embryosac nucleus, and the antipodal cells are formed the same as in Monotropa. In Orchis pallens, Strasburger (1) finds no development of endosperm further than the endosperm nucleus. This nucleus disintegrates during the early development of the embryo.

Strasburger (2) thinks that Monotropa is as good as Orchis or even better as material for study of the embryosac, and is more easily secured. This is of course in consideration of his location and the methods at his command in 1877. He finds that the development of the embryosac and embryo is the same, even in almost all details, in the two plants; and thinks therefore that, since the plants belong not only to different families but to different divisions of the Phanerogams, his results may be of universal signification.

The Endosperm in Myosurus minimus, Fritillaria imperialis, and Reseda odorata.

The development of the endosperm in Myosurus minimus is described by Strasburger. (3) His method is to kill and harden the ovules in alcohol and then with needles dissect out the

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(1) Strasburger, l.c., p, 70.
(2) " " " 33.
(3) Dr. Edward Strasburger, Botanische Practicum, p, 531.

endosperm, which often in this way may be gotten out in thin strips. In the embryosac of Myosurus which Strasburger describes, he finds a large one-celled embryo. It is close to the the micropylar end of the embryosac, and its cell wall is elongated making it appear like a tubular sac. Remnants of the synergidae remain and the antipodal cells are in good condition. In this embryosac he finds a parietal layer of granular protoplasm in which there are a number of free nuclei all in the same stage of karyokinetic division. (1) In a sectional view these free nuclei seem to lie at regular intervals in a chain or string of protoplasm. In a surface view the protoplasm appears as a sheet with the nuclei arranged at the same quite regular intervals. Later in the development progressive cell division takes place in this parietal layer of protoplasm and free nuclei. One cell for each nucleus is formed. Prior to and during this process of cell formation in the parietal layer, other free nuclei are formed on all sides toward the center of the embryosac. This process of free nuclear division followed by cell formation is continued until the whole embryosac is filled with endosperm tissue.

Strasburger (2) has described free nuclear formation

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(1) Strasburger, l.c., 209,a.
(2) " " p, 314.

followed by cell formation as found in the development of the endosperm in Fritillaria impirialis. He fixed the entire tissue of the ovules by immersing them in absolute alcohol. Then, placing them in a mixture of one-half each of alcohol and glycerine, he was able with needles to pick or tease out thin strips of the developing endosperm. For staining he used Hämatoxylin and Safranin. He mounted his specimens in balsam. The strips of endosperm thus secured and stained came from the embryosac in its earlier stages of development. All stages of the mitotic figure in free nuclear formation were found. Strasburger(1) represents in one figure spirem, equatorial plate, diastral, dispirem, and cell-plate stages. This cell-plate soon disintegrates and has therefore nothing to do with the later development of the cell walls(2). The cells of the endosperm are finally formed by progressive cell division.

In Reseda odorata, Strasburger(3) found the development of the endosperm much the same as in Fritillaria imperialis. Cell division is due to the formation of cell-plates in newly formed nuclear spindles. A cross-section of a seed in which

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(1) Strasburger, l.c., Fig., 218.
(2) " " " 219.
(3) " " p., 319.

the endosperm is fully developed shows a radial arrangement of endosperm cells.

Strasburger (1) says that from a study of Monotropa Hypopitys, Myosurus minimus, and Fritillaria imperialis it may be seen that endosperm is formed in two general ways: in Monotropa we have cell formation in the endosperm by ordinary cell division accompanied by indirect nuclear division, while in Myosurus and Fritillaria free indirect nuclear division takes place and is followed sometime afterward by progressive cell formation. He says this is because in the first case, as in Monotropa, the increase in size in the embryosac is quite slow and never large, while in cases cases of free nuclear formation the embryosac grows very rapidly.

Endosperm Formation in Taxus baccata. (2)

In his description of the embryology and endosperm development of Taxus, Jager represents one or several embryosac-mother-cells in the nucellus. The mother cells divide into three or four cells and one of these daughter cells becomes the embryosac. Sometimes there are two embryosacs in one ovule but only one comes to maturity. (3)

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(1) Strasburger, l.c., p., 320.

(2) L. Jager, Beitrage zur kertniss der Endospermbildung und zur Embryologie von Taxus baccata. L. Plates XV-XIX, Flora

(3) Jager, l.c., Figs. 7,8 and 10. Pl. XV. (Aug. 1899.

In this embryosac a number of free nuclei are soon formed by indirect division. These free nuclei occupy a parietal position in the embryosac. (1) Jäger represents eight in one figure and thirtytwo in another, but the number becomes much greater. He mentions two hundred fifty-six. As these endosperm nuclei increase in number, the embryosac increases in size by encroaching on the nucellar tissue. The cells of the nucellus disintegrate as the embryosac enlarges.

When the free endosperm nuclei have increased to the number mentioned above, a single layer of parietal cells is formed with one nucleus in each. In section these cells are at first nearly square. (2) But they soon become elongated toward the interior of the embryosac. They are now triangular with the more acute angle extending inward. The free nuclei have all been included in the formation of these cells, and now the nuclei of the cells migrate toward the acute angle. The cells grow larger and soon divide by the ordinary cell division, the nuclear division being indirect. The new cell wall thus formed is tangential to the wall of the embryosac. These divisions continue until a row of cells is formed which ex-

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(1) Jäger, l.c., Figs., 12 and 13, p. 252.

(2) " " " 13 " 17.

tends to the center of the embryosac. Some of the original cells, however, do not divide because they lack room. Others divide only once or twice. Most of the cells are found to be smaller as one proceeds toward the center of the embryosac. (1) Jäger represents these stages of development in cross and longitudinal sections. All of the stages present a radial appearance, but more especially that in which the endosperm cells completely fill the embryosac to the center.

Toward the end of May the endosperm having grown so as to fill the embryosac, the archegonia are formed in it. There may be two or three or more archegonia and two or three may be fertilized; but it is very seldom that more than one embryo finally developes.

When fertilization has taken place, the endosperm cells increase in number rapidly by division. The endosperm fills the embryosac which continues to encroach on the nucellar tissue until all of its cells have disintegrated. A cylindrical body of them which extends from the region of the embryo to the chalazal end of the endosperm are smaller than the others in other parts of the embryosac and they stain

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(1) Jäger, l.c., Figs. 18-22, Pl., XVI.

more densely . It is probable that this cylinder of endosperm cells has something to do with the transmission of nutritious materials.(1)

At the end of June and the beginning of July, (2)Jäger noticed one and two nuclei in the endosperm cells. By the ninth of July he could count three, four, five and six nuclei in some cells; and on the 28th and 30th of July, fourteen and sixteen. He saw the karyokinetic figure in many cases and believed that all the nuclear divisions were indirect. The nuclei of these multinucleated cells were distinct in outline and showed nucleoles clearly. At the beginning of Sept. these nuclei lost their distinct appearance and became massed together into two or three groups in each cell.

After fertilization the endosperm tissue became richer in protoplasm and charged with food materials. As the embryo developed it used up some of the endosperm and especially that between the cotyledons.

Materials.

Most of my material of Monotropa hypopitys was furnished me by Dr. R. A. Harper. The ovules of Iris versicolor were furnished by Mr. H. G. Timberlake. In addition to these ovules

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(1) Jäger, l.c., p.257 and Figs. 23,27.
(2) " " " 258.

he furnished me also a number of prepared slides of Iris. The material used in the study of Monotropa and Iris is more fully described below.

The ovaries and ovules of the "Paper White" Narcissus were most of them collected at the greenhouse, Madison, Wis. in Nov. and Dec. 1899. In the collection of this material an attempt was made to secure young flowers, oldflowers and young fruits. But the search for endosperm in Narcissus was unsuccessful. The ovules seemed not to have developed so far as to be ready for fertilization. Abortive materials only were found. The ovaries were found to be easily sectioned so as to secure longitudinal sections of them.

Ovaries of Impatiens Sultani were secured at the greenhouse belonging to the Horticultural department of the Univ. of Wis. These specimens could without difficulty be sectioned so as to produce fine views of the embryosacs. Very few of the ovules, however, showed any positive sign of normal development. Ovaries of Lycopersicum esculentum were also secured at the Univ. greenhouse. In these specimens the ovules were pretty small to work with; and yet, if they could have been cut so as to produce a number of good longitudinal sections, they might have proved valuable. Radial sectioning

of the ovaries was tried; but even this method produced only a few longitudinal sections.

Methods.

Material was fixed in Flemming's Stronger fixing solution; in Flemming's Weaker solution; in Merkel's fixing solution; and in Iridium Chloride. Those fixed in the Flemming and Merkel solutions were satisfactory; all tissues were well preserved. The Iridium Chloride did not do so well. The objection to its use with these tissues seems to be that, they are too old and firm on their surfaces, and too large for that solution to penetrate them readily. The specimens were left in the fixing fluid 48 hours. They were then washed in running water about 6 hours; and immediately afterward put through 15, 30, 50, 70, 80, 93, and 100 per cents of alcohol. They were not left in the lower and higher grades of alcohol more than 20 to 30 minutes. They were now placed in a mixture of alcohol and chloroform and then in pure chloroform. This was followed by soft and then hard paraffin in the paraffin oven.

After imbedding the ovaries, or the ovules separately in the case of their being large, in paraffin, and cutting sections on the microtome, the sections were fastened to the slide by a mixture of the white of an egg and glycerine. The specimens

were stained on the slide in Flemming's triple stain, and mounted in balsam. By means of these methods the tissues were well differentiated. One could easily distinguish cell walls, protoplasm, kinoplasm, nuclear membrane, nucleoles, ids, linin and chromosomes.

Monotropa hypopitys.

The ovules of Monotropa hypopitys grow on a central placenta. They are small and anatropous and crowded together. Their longest axes are in general at right angles to the main axis of the ovary. Hence, a great majority of the ovules may be cut longitudinally by making a cross-section of the ovary. The ovary, or pod, has five cavities. This and other structural appearances, which a cross-section shows indicate that it arises from five carpels.

Figures one and two represent an early stage in the development of the embryosac of Monotropa. In number two it is magnified 1000 diameters. The nuclei of the cells, a and b, according to Strasburger (1) are the result of a division of one of the daughter nuclei of the proembryosac nucleus or, as Hofmeister (2) in his work on the higher Cryptogams first called it,

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(1) Strasburger, Befruchtung und Zelltheilung.

(2) Hofmeister, Germination, Development and Fructification of the Higher Cryptogamia, and the Fructification of the Coniferae, Trans. by F. Currey.

the macrospore-mother-nucleus. These two cells, as the process of development continues,disintegrate and become flattened and pushed together forming a dark cap on the micropylar end of the embryosac as at a in figure 3. The nucleus at c in figure 2 is the other of the two daughter nuclei of the macrospore-mother-nucleus. This nucleus with a large quantity of kinoplasm and cytoplasm, and a few vacuoles, occupies the large cavity in the figure, the embryosac. The nucleus is in the equatorial plate stage of division and the kinoplasm is in a threadlike condition froming a nuclear spindle. The end of the spindle whcih is toward the chalazal end of the embryosac appears to be multipolar. In this equatorial plate stage parts of many of the chromosomes may be seen very distinctly. The darkly stained portions of tissue on the margin of the embryosac are parts of the thin nucellar tissue which seems to have a great affinity for the gentian violet of the triple stain.

When the division of this third nucleus of the macrospore-mother-cell is completed the condition represented in figure 3 is soon reached. The nuclei appear in a resting condition, and the nuclear membrane, the ids, and linin may be seen distinctly. This may be called the two-nucleated stage of

the embryosac. Figure 4 also shows the two-nucleated stage; butslightly more advanced in development. The nuclei are in the first stage of division, the spirem. In these the nucleoles are quite apparent. In figure 4 the light-refracting cap is not so distinct as in figure 3. Figures 5 and 6 are representatives of the four-nucleated stage of the embryosac, each nucleus of the two-nucleated stage has divided to produce this four-nucleated stage. In figure 5 all of the nuclei lie in the same straight line, the main axis of the embryosac. In figure 6 those nuclei at the micropylar end are in the main axis; but those at the chalazal end are in line almost at right angles to this axis.

As the embryosac continues to develope, we have the condition represented in figure 7. Here the four nuclei are in late stages of division. The one at a in its half nearer the chalazal end of the embryosac shows the diaster stage very clearly; the others are in the dispirem stage. The cell plate is prominent in each of the four divided nuclei. The nucleus (b fig 7) nearest to the chalazal end of the embryosac has the long axis of its spindle at right angles to the longest axis of the mass of protoplasm in which it lies. This can be said of the nucleus

at the other end of the embryosac. But these last facts are contrary to Hertwig's second law: "The two poles of the division figure come to lie in the direction of the greatest mass of protoplasm." (1) Again, the pair of nuclei (a and b fig. 7) nearer the chalazal end of the embryosac, and also the pair at the other end, have their division planes at right angles to each other within a few degrees. Since each of these pairs of nuclei arose from the division of a nucleus in their part of the embryosac, both nuclei of each pair can not have their plane of division at right angles to the plane of the next previous division. Hence, one of each pair of these nuclei cannot conform to (2)Hertwig's third law: "The axis of the second division spindle would never in such a case place itself in the direction of the preceding division spindle, but rather at right angles to it." Figure 8 represents about one half of an embryosac of the same stage of development. In this the same relative position of the two nuclei exists; but they are not so near the micropylar end of the sac, nor is their relation to the main axis the same as in the other figure. The exact position of

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(1) Dr. Oscar Hertwig, The Cell, Trans. to Eng. by H. J. Campbell, M.D., p. 217.

(2) Hertwig, l.c.,p., 220.

the nuclei in the embryosac does not seem to be important. Mottier (1) finds in his study of the embryosac of the lily that the cell plates formed at this stage continue their development and by means of them the cell walls of the synergidae and egg cell are formed. This does not seem to be the case in Monotropa; for in figure 9, which in a little later stage of the embryosac, these cell plates do not appear.

Figures 9 and 10 represent the eight-nucleated stage of the sack. It appears in two figures because what is represented was found in two adjacent sections; and this is due to the fact that the microtome sections of the ovule were not exactly longitudinal. The three nuclei which are probably destined to become the nuclei of the synergidae and egg cell, and the protoplasm which surrounds them are not enclosed in cell walls. The antipodal nulcei and their surrounding protoplasm are inclosed in cell walls, thus becoming cells. These nuclei are dense and small. One polar nucleus is present; also a part of the others. In figure 11 we have represented the greater part of the embryosac, the micropylar end being

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(1) Jahrbücher für Wissenschaftcl Botanik, Vol., 31, p., 125.

present. In this the two polar nuclei have approached each other and are about to fuse. In figure 12 this fusion is represented as having taken place; and in both of these embryosacs the cells designated as sysergidae and egg cell show distinctly a surrounding plasma-membrane. There is, however, no indication that fertilization has taken place. Only one of the antipodal cells appears in figure 12.

Very soon after fertilization has taken place, the oöspore becomes tubular and grows from the micropylar end of the embryosac down into the same and close to one side, (fig 13). This indicates that the embryo finally takes its place among the endosperm cells (fig. 15, a)by growing around the endosperm cell nearest the micropylar end of the embryosac and up between the next two endosperm cells; and that the embryo does not break through the wall of the first endosperm cell as Strasburger thinks. (1)

The synergidae (fig. 13) have disintegrated, neither do the antipodal cells appear. But the nucleus which was the result of fusion (fig. 12), the embryosac or endosperm nucleus, has divided (fig. 13) and a cell wall has been put across the em-

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(1) Befruchtung und Zelltheilung, p., 98 and fig. 140, Pl.IV.

bryosac separating the two resulting nuclei and dividing the embryosac, aside from the embryo, into two cells. These are the first two cells of the endosperm. Strasburger(1) represents this and the following division of the endosperm cells as indirect division, a division in which the mitotic figure is distinct and in which the cell plate is continued to form the cell wall.

Figures 14 and 15 represent the embryosac at a stage in which the endosperm is nearly or quite complete. The sections give us a circular or nearly circular view of a body not in the center of the embryosac but nearer the micropylar end; This is the embryo and consists of at least two cells and probably four or more. On the side of the embryo toward the micropyle the sections represent one or two cells of the endosperm. In figure 14 the embryo seems to be imbedded in the next endosperm cell but in the other section there is an endosperm cell on either side of it. Then, toward the chalazal end from the embryo there are three or four cells. It is probable that there are not less than eight or more than eleven cells in all in the endosperm;- one cell at the chalazal end of the embryosac, four in the next series, two or four in the

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(1) l.c., figs. 135-140, Pl. IV.

next, and one or two at the micropylar end. These endosperm cells are large and plump. The nuclei are large, but not so prominent as those of the embryo. It does not appear that the embryo in its growth has as yet consumed much, if any, of the endosperm.

Iris versicolor.

The ovules of Iris are arranged in double rows in the three cavities of the ovary. They are anatropous and lie in the cavities of the ovaries so that the raphes of any two of about the same height in one cavity, are adjacent to each other. This condition might make one think of them as lying back to back. As the ovules grow and become rapidly developing seeds, they crowd each other greatly. They become angular, taking the shape of the space that each is able to find for itself, so that when they are well developed into seeds they are very irregular. In this condition one finds it difficult to distinguish, from an exterior view, one part from another(figure 27 & 28). The young ovules, however, are quite regular and show the outer and inner integuments distinctly (figures 16 & 19). During the earlier stages of development the nucellus tissue is quite a large portion of the tissue of the ovule (figure 1c,a, and 24, a). And this tissue is very persistent,

for some of it is still found in seeds that are nearly full grown (figures 27 and 28,a).

In the outer integument and especially in the chalaza, there are many cells partly or entirely filled with a substance that stains very densely(figures 29,a and b; 28, b; and 23, a). The protoplasm and nuclei of these cells have their usual appearance in cases in which they have not been entirely crowded out by this substance (fig. 35.)

The embryosac of these ovules is situated but one layer of cells deep in the nucellus at the micropylar end and extends centrally into the nucellus. The nucellus is continually thicker about the embryosac as one looks toward the chalazal end. The embryosac is curved considerably corresponding to the curve of the anatropous ovule (figures 16 and 13). The embryosac at the time of fertilization and later is very irregular in outline as one may see by comparing figures 17 and 18. The figures represent sections of the same embryosac. They are not adjoining sections but are not more than three or four sections apart. The irregularity of the embryosac in later growth may be observed by referring to figures 19, 20 and 24. The increase in size of the embryosac has two causes:

the growth of the ovule and the disintegration of its walls and the nucellar tissue. The walls and the nucellar tissue do not break down with equal ease in all parts. This is nicely illustrated in fig. 20, a in which the chalazal end of the original embryosac forms a caecum in the sac of the later stages of development. The rudiments of the antipodal cells may still be seen in this caecum. The irregularity of outline is at least partly due to this unequal disintegration.

Figure 18, b represents the egg cell, the rudiments of the synergidae at c, and the embryosac nucleus(a) in a stage of indirect division. The chromosomes are very apparent. In figure 17, a the embryosac nucleus is plainly in the equatorial plate stage of mitotic division. The barrel shaped spindle is also plainly to be seen here. This figure is a more central section of the same nucleus that is represented in figure 18, a. Considerable protoplasm is found in the region of the embryosac nucleus.

The first stage of the endosperm formation in Iris is a free nuclear formation. The division of the embryosac nucleus(fig. 17, a,) is followed by a large number of indirect divisions of the daughter nuclei. The nuclei so produc-

ed occupy a parietal position in the embryosac in a sheet of granular protoplasm (figures 19-24). When the embryo has developed to eight and sixteen cells, there are four to six of these free endosperm nuclei in a single longitudinal median section of the embryosac (figures 19 and 20). . When the embryo has come to consist of thirty-two to sixty-four cells, the endosperm nuclei are greatly increased; there are fourteen to twenty-four in a single longitudinal median section of the ovule (figures 21-23). During these early stages of the development of the endosperm all of the nuclei in any one embryosac are is the same stage of rest or division. Figure 36 is a sketch of a nucleus of the endosperm of the same section as figure 22. It is multiplied 1550 diameters. This nucleus is at about the equatorial plate stage of division and shows the splitting of the chromosomes. All of the endosperm nuclei in the sections of this ovule are in that stage of division. In a later stage of development these free nuclei are much more numerous (fig. 24). They are found in greater numbers in the region of the embryosac where the nucellar tissue(fig. 24,a) is most abundant. The nuclei in this region are represented in figure 31, multiplied 425 diameters. They lie in a sheet, or, if one considers only the sectional view, a

band of granular protoplasm. It will be noticed that they are in a resting condition. This is true of all sections of the ovule in question. In shape these nuclei are ameboid and, as ameboid nuclei were often found in this position and in no other in this material, it is probable that they have to do with the transmission of nutritive material from the nucellar tissue.

In all of the ovules examined the condition of the nucellar tissue shows that it is disintegrating and its product is being utilized for the support of the developing endosperm. The nucellar tissue all about the developing endosperm presents a ragged edge in section(figs. 13.24). Figure 25,*a* represents this edge of the nucellus as found at *a* fig. 22, multiplied 425 diameters. The cellulose walls are all that remain of those cells nearest the endosperm. Parts of the nuclei and protoplasm have gone from those a litle more remote. Those still more remote are in a normal condition. The same conditions exist in the nucellar tissue that remains near the chalazal end in the older ovules, only more intensely so as may be seen by referring to figure 32 which is a detailed description of a portion of this nucellus found at *a*, fig. 28.

In a considerable later stage of the development of the endosperm than that described above, cell formation is found to have taken place (figures 29, 30, and 37). More commonly than otherwise the endosperm cells are arranged radially in the embryosac. There is also generally a cavity in the interior (fig. 28). Some sections, however, do not show much of the radial structure (fig. 26). One set of sections showed radiations of the endosperm cells like the rays of a palm leaf fan (fig. 27). It is probable that these sections lacked thirty or forty degrees of being longitudinal. Still, this could hardly account for the difference between the radial and fan structure. Figure 37 gives a detailed view of the appearance of the endosperm as seen at e, fig. 28. One of the nuclei is in a state of mitotic division. The arrangement of the cells in the region of the embryo is very irregular (figures 29-30). Immediately next to the embryo the cells of the endosperm are disintegrating. It is probable that the product of this disintegration is being used to nourish the embryo. These endosperm cells are not very rich in protoplasm and food material at this stage of their development. But the endosperm next to the nucellus in the region of the chalaza is quite dense with protoplasm (fig. 34). The nuclei in this

part are more or less ameboid and there are two of them in some of the cells. In some cases these two nuclei seem to be fusing. Cell division in this region is not quite complete. In some of the sections free nuclei and protoplasm lie between the endosperm and the disintegrating nucellus tissue of the chalazal region (b, a, and c, fig. 33). These nuclei are in most cases very irregular and the stain gives them a slightly cloudy appearance. Evidence is quite strong that these free nuclei and the protoplasm are not a part of the endosperm or of the nucellar tissue. It is possible that they are derived from the antipodal cells. And again it is possible that they have the same origin as like nuclei and protoplasm described by Schaffner(1) as observed in Sagittaria. He finds in Sagittaria that a division wall is put across the embryosac immediately after the first division of the endosperm nucleus, and that "partition" is permanent. The daughter nucleus on the micropylar side of this wall goes on in the usual way to the formation of many free nuclei. The nucleus on the antipodal side divides later on so as to form two or three or possibly more nuclei. All these latter are much enlarged. No further development was noticed; but after cell formation had taken place on the micropylar side of the of the "partition"

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(1) Endosperm of Sagittaria variabilis,- Bot. Gazette, Apr. 1897, p., 250.

wall, these three or more cells took a very deep stain. Schaffner thinks these three or more cells may have something to do with the transmission of nutritive substances. In Iris (fig. 35, c) there is evidence that we have a similar condition and use.

Many of the cells of the endosperm of the advance stages described above (figs. 28, 29, 30 and 37) are in very active division stages. The endosperm cells that are dividing are those lying toward the outside of the endosperm mass in all directions; and more especially toward the chalazal region, but not immediately bordering upon it. No cell division was observed in the region bordering on the central cavity; or in the center of the endosperm mass when no cavity existed. These dividing cells exhibit very beautiful mitotic figures in all stages (figures 38-45). In some of the earliest stages of division observed kinoplasmic fibers are lying in all directions close about the nucleus, giving the appearance of a zone of felt (fig. 38). These are the fibers that a little later form the barrel shaped spindle (fig. 39). The nuclear membrane may still be seen, also a large nucleole; but the latter has not the usual dense appearance. It is probably on the verge of disintegration. The chromatin thread has shortened

and thickened, but the ids in it still show quite distinctly. The felted zone condition is decided evidence that a centrosome does not exist here, for the kinoplasmic fibers, extending in all directions as they do; plainly, do not come from a centrosome. The fact that the spindle is barrel shaped is also opposed to the possibility of the presence of the centrosome. The equatorial plate stage of mitotic division (figures 39-40) presents a large number of chromosomes. The split condition of the chromosome is very apparent in some cases. The fibers of the spindle are marked and show quite decidedly in many cases their attachment to the chromosome.

Figures 41-42 represent a metaphase of mitotic division. Each split chromosome has been separated, one half going to one pole and the other half going to the other pole. The retreat to the region of the poles is in progress. The dispirem state is one of the anaphases of indirect division(fig 43). In this case the formation of the cell plate is well begun. The kinoplasmic fibers are beginning to thicken in a plane at right angles to the axis of the barrel spindle ; and additional fibers are being formed on all parts of the equatorial zone so formed for the purpose of extending the thickening in these fibers in all directions in the plane. The formation of these new or additional fibers seems to be in-

fluenced by the nuclei; for the new fibers are kept in connection with the nuclei of other fibers. This process continues until a cell wall is formed between the daughter nuclei and extends around to the walls of the mother cell (figures 41-45). Cell division is here completed.

General Summary and Discussion of Theories.

Material secured at greenhouses is as a rule unsatisfactory for the study of endosperm formation. One should secure ovules from plants that are growing and reproducing in their natural environment; for such ovules are less likely to be abortive.

Endosperm in Monotropa consists of a few cells, probably not more than eleven. They are plump, being well filled with food material. These cells arise from the endosperm nucleus. The division of the nucleus is indirect and is accompanied by cell division. No free nuclear formation takes place.

During the development of endosperm in Iris the nucellar tissue disintegrates. The protoplasm of the growing endosperm is most dense in the region of the nucellar tissue; and the nuclei in this part of the endosperm are ameboid and enlarged.

These facts seem to show that the disintegrating nucellus is being used by the endosperm for nutrition.

The free nuclei of the early growth of endosperm in Iris are parietal in position. In whatever condition of rest or division one of these free nuclei of a given ovule may be found; all others of the same ovule will be found to be in the same condition.

After the cell formation which follows free nuclear formation in Iris is completed the endosperm continues to develop by ordinary cell division. These dividing cells are very beautiful specimens for the study of the phenomena of indirect nuclear division. They show many facts of this division just as well as the cells of the onion root tip or the pollen-mother-cells of the larch. The felted zone stage described above (fig. 38) affords decided evidence for the confirmation of the theory that the spindle in mitotic division in plant cells is not formed from a centrosome or central body. In the felted zone the kinoplasmic fibers extend in a great variety of directions tangential to the spherical nucleus. This shows plainly that they do not originate from the poles. If centrosomes were present, the fibers would come from two or possibly more poles; but it is incon-

ceivable that if they come from the centrosomes, they should lie in such a great variety of directions. Unless, indeed, there were as many centrosomes as fibers which is altogether unlikely. The felted zone is followed by the multipolar spindle stage; but even then no centrosome is visible. When the spindle in the endosperm cells of Iris is formed, it is barrel shaped (Fig. 33) instead of double cone shaped as in animal cells where the centrosome exists. If the centrosome exists with the barrel shaped spindle, there must be one at each end of each fiber or bundle of fibers; but this is improbable. None are visible at any rate in the endosperm cells of Iris although the cells are so stained as to produce extremely sharp, bright figures.

The mitotic division of the endosperm cells in Iris affords confirmation also of the theory that the daughter nuclei control the formation of the cell plate and that it has its beginning in a central position in the mother cell and in the progress of its formation extends from the central position in all directions in the equatorial plane toward the walls of the mother cell (Figures 43-45). The fact that kinoplasmic threads are constantly extended from the daughter nuclei to all new and extreme points of the cell plate indicates the influence of

the nuclei in the process. The daughter nuclei do not stand in the early stage of cell plate formation very near one cell wall of the mother cell and migrate to the opposite one as the plate is formed as Treub(1) has observed, but in all stages of the plate formation they occupy a central or nearly central position in the mother cell, as may be observed by referring to the figures.

The function of endosperm is the nourishment of the embryo during its development and especially during germination. Of course, there are cases like that of Orchis in which the endosperm is merely rudimentary and therefore can have no use. Then, there are a large number of cases of dicotyledonous angiosperms such as the gourds and others in which all of the endosperm is utilized in the development of the embryo; hence, none will be left for the support of germination in such cases. In Iris the disintegration of the endosperm in the region of the embryo and not in other places (figures 15, 29 and 30) is good evidence that the embryo is nourished by it during development. The facts that the endosperm cells in mature seeds (Fig 14) are large and well supplied with food material and that during germination some part of the young plant remains for some time

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(1) Lehrbuch der Botanik, Dr. Eduard Strasburger, [illegible], 6 .

in connection with the endosperm, so to show that the endosperm is used in germination for the support of the embryo.

Let us now consider the morphology of endosperm. The prothallia of Ferns and Equisetaceae, after the embryo is formed in their archegonia, are used for the support of the young sporophyte. In the heterosporous Equisetaceae the prothallia were female. In such heterosporous cryptogams as Marsilia and Selaginella the female prothallia remain partly enclosed in the macrospores and are also used for the support of the young sporophytes produced in their archegonia. If we now pass to the gymnosperms, it is found that the macrospore, or embryo-sac, is entirely enclosed in the nucellus or true macrosporangium and that the prothallus, or endosperm, remains entirely enclosed in the macrospore. This prothallus, again, is of course female and it is used for the support of the embryo, or sporophyte, produced in its archegonium. The prothallus in the vascular cryptogams and the gymnosperms arises from one of the four cells derived from the spore mother cell. And the prothallus therefore is the gametophyte generation in all of these cases. In angiosperms we find the macrospore, or embryo-sac, entirely or partially enclosed usually in the macrosporangium, or ovule, but the gametophyte generation in this embryo sac is very much reduced as compared with that found in the gymnosperms

gymnospermae. It is probable, however, that the gametophyte, the prothallium of ferns and coniferae, is represented by the antipodal cells in its earlier stages and by the endosperm in its older stage. If the antipodal cells may be considered as a prothallus, the synergidae must form its archegonium and the egg cell, the oöspore of that archegonium. And the embryosac nucleus must be a part of this prothallus, the part which, when developed, is homologous with the older prothallus of the fern or of Taxus baccata.

It seems that it has been fairly shown above (1) that the endosperm is homologous in function with the older stages of the prothallium of the vascular cryptogams and the prothallus, or endosperm of gymnosperms. that these prothallia are female, and therefore, that the endosperm of angiosperms is a female prothallus;- (2) that these homologies probably hold morphologically and for this reason the endosperm of the angiosperms is probably a female prothallus.

The reduction of the chromosomes in ferns takes place in the second division of the spore mother cell to produce the four spores. Hence, the prothallus, or gametophyte, has the reduced number of chromosomes throughout its life. Since this is true we have a right to infer that the gametophyte,- th

antipodal cells, the synergidae, the two polar nuclei, and the egg cell,- in angiosperms has a reduced number of chromosomes. The embryo secures the double, or sporophyte, number of chromosomes by the fusion of fertilization and might it not be that the fusion of the polar nuclei is for the purpose of securing this sporophyte number of chromosomes? If this is the purpose of the fusion, it must be that the doubled number of chromosomes is of advantage to the plant; and it may be of advantage to the plant for the endosperm which has considerable work to do in storing and transmitting nutritious substances and the nucleus is the dynamic center of the cell.

The great showing for numbers of chromosomes that the endosperm cells of Iris (Figure [illegible]) had, should lead one [illegible] to think that the number of chromosomes are not only been doubled but tripled. It must be that they are tripled, if the observations of Guignard (1) and Nawaschin can be confirmed. They find that the cells enter the embryo-sac from the pollen tube, that these cells are motile, and that one fuses with the egg cell and the other with the polar nuclei. [illegible]

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(1) Uber die Antherozoiden und die doppelte sexuelle Copulation bei den angiospermen Gewächsen. Comptes rendus. 1899. T. CXXVIII, p., 864,- reviewed in Naturwissenschaftliche Rundschau. 1899, Nr. 35, IV Jahrg.

chromosomes are tripled in the endosperm of angiosperms, may it not be for dynamic purposes? This matter of the chromosomes points to the idea that the endosperm of the angiosperms is not morphologically homologous to the older prothallus of vascular cryptogams and gymnosperms; but that it is a new tissue peculiarly adapted to this higher class of plants.

As [illegible] said above the endosperm of some plants is [illegible] and in others it is all used up by the embryo by the time that the seed is fully developed. But in the latter case the food that would otherwise be stored in the endosperm for the support of germination is now stored in the cotyledons. When none of the endosperm persists to the time of the ripening of the seed, the embryo is generally small and enclosed in the endosperm in the axis of the seed and near the micropyle. Or the embryo may be entirely outside of the endosperm. With the exception of the embryo and food tissues the central cavity and [illegible] [illegible] is [illegible] [illegible]. The [illegible] cell walls in some seeds become very thick and hard or stony. Examples of this are [illegible] ivory. In other plants, [illegible] cytoplasm, [illegible] [illegible] [illegible] [illegible] [illegible] of [illegible] [illegible]. [illegible] [illegible] [illegible]. From [illegible]

[illegible].

The nuclear formation is the first stage in the development of endosperm in Iris. This is followed by progressive cell formation which is [illegible] cells [illegible] about [illegible] leaving a small central cavity. After progressive cell formation is completed, the endosperm continues to develop by ordinary cell division chiefly in or toward the parietal region of its [illegible]. This last step in the formation of the endosperm found in Iris has not been described [illegible] in [illegible]. [illegible] the endosperm formation in [illegible] the same; but here the progressive cell formation is only [illegible] which is [illegible]cular. In [illegible] as indicated above, the endosperm formation is by ordinary cell division; that is, by nuclear division or [illegible] immediately followed by cell division. The [illegible] formation followed [illegible] by progressive cell formation seems to be a [illegible] taking a large amount of work [illegible] short [illegible] and this is [illegible] probably [illegible] of Iris. [illegible] of [illegible] in [illegible].

[illegible] that the endosperm of Iris [illegible] nt [illegible].

that the cell division [illegible] the [illegible] [illegible] [illegible], [illegible] know that the endosperm, after a certain stage in the devel- opment, increases in volume by [illegible] [illegible] [illegible] of its cells instead of [illegible] [illegible] [illegible] [illegible] [illegible] [illegible]. The "certain stage" is probably [illegible] just at the close of the cell formation that follows free nuclear formation.

It is probable that the tissues lying next to the endo- sperm and nucellar tissue in their [illegible] concerned in nutrition, [illegible] as [illegible] [illegible] [illegible] especially on account of [illegible] con- dition of [illegible]. [illegible] [illegible] [illegible] in [illegible] [illegible] other [illegible] [illegible] [illegible] [illegible] [illegible] [illegible] [illegible] [illegible] [illegible] [illegible] [illegible] [illegible] [illegible] to do with nutrition.

[illegible] [illegible] during [illegible] [illegible] of this [illegible], I have [illegible] many valuable suggestions [illegible] Dr. R. A. Harper [illegible] [illegible] [illegible], [illegible] S, both of the Botanical Laboratory of the University of Wisconsin.

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Explanation of Figures.

These figures were drawn with the aid of the camera lucida and 1/16 oil immersion objective, and with the Leitz oculars.

Monotropa hypopopitys.

Fig. 1. Longitudinal section of the three daughter cells of the macrospore-mother-cell, X 425.

Fig. 2. Same as fig.1, X1000. a and b the two cells that become the embryosac cap. c embryosac with nucleus in equatorial plate stage of division.

Fig. 3. Two-nucleated stage of the embryosac, X 680. a embryosac cap. Nuclei in the resting condition.

Fig. 4. Two-nucleated stage of the embryosac, X 425. Nuclei in the spirem stage of division.

Fig. 5. Four-nucleate d stage of the embryosac, X 425. a embryosac tissue. b cap.

Fig. 6. Four-nucleated stage of the embryosac, X 680. a embryosac tissue. Nuclei in the resting stage. b nucleole.

Fig. 7. Embryosac, showing transition from four-nucleated to eight-nucleated stage, X 620. a and b nuclei in cell plate stage of division. c micropylar end of embryosac.

Fig. 8. Part of embryosac in the same stage of development as that of fig. 7, X 620. a cap.

Fig. 9. Part of the embryosac of the eight-nucleated stage, X 620. The upper part of this embryosac is represented in fig. 10. a synergidae. b egg-nucleus of the antipodal cells.

Fig. 10. Part of the embryosac in the eight-nucleated stage, X 620,- See fig. 9. a one of the polar nuclei. b the other two antipodal cells.

Fig. 11. Part of the embryosac, X 425. a polar nuclei at the point of fusion. b egg-cell. c synergidae. e cap.

Fig. 12. Embryosac after fusion of polar nuclei X 240. c embryosac or endosperm nucleus, which resulted from the fusion. a egg-cell, or oosphere b synergidae. d one of the antipodal cells.

Fig. 13. Embryosac showing the two-celled stage of the endosperm, X 240. a fertilized egg, or oospore. The cell wall has grown tubular. b endosperm cell. c cell wall across the endosperm separating the two endosperm cells.

Fig. 14. Longitudinal section of young seed presenting five endosperm cells, X 240. e two cells of the embryo.

a part of the embryosac not filled with endosperm cells

Fig. 15. Longitudinal section of young seed showing eight endosperm cells, X 240. a embryo. b and c parts of the embryosac not filled with endosperm cells.

Iris versicolor.

Fig. 16. Longitudinal section of ovule, X 45. a nucellus. b micropyle. c outer integument. e embryosac. f raphe.

Fig. 17. Longitudinal section of embryosac, X 220. a embryosac or endosperm nucleus. b one of the antipodal cells.

Fig. 18 Longitudinal section of embryosac, X 220. a endosperm nucleus. b egg-cell, or oosphere. c one of the synergidae.

Fig. 19. Longitudinal section of young seed, X 45. a young embryo. b embryosac containing, beside the embryo, six endosperm nuclei. c disintegrating nucellar tissue.

Fig. 20. Section of young seed, X 45. a caecum containing antipodal cells. b disintegrating nucellar tissue. e embryo. en endosperm.

Fig. 21. Young seed, other than in figures 19 and 20, X 25.

Fig. 22. Young seed, same age as in fig. 21, X 45. a disintegrating nucellus tissue. b endosperm nuclei and protoplasm, probably shrunken from the parietal position by fixing.

Fig. 23. Young seed, showing again how the free nuclei and protoplasm have fallen away from the parietal position, X 45.

Fig. 24. Young seed in longitudinal section considerably older than that of figures 21-23, X 45. a nuecllus. c chalaza. b free endosperm nuclei in parietal position.

Fig. 25. Some details of the disintegrating nucellus, taken from the point marked a fig. 22, X 425. a disintegrating nucellus. b dividing line between the nucellus and the inner integument.

Fig. 26. Longitudinal section of seed, considerably older than that of fig. 24, but not as yet fully developed, X 25. a densely stained cells in chalazal region. e embryo. en very slight radial arrangement of endosperm cells. i inner integument.

Fig. 27. Section of seed, probably within 30° or 40° of being longitudinal, same age as that of fig. 26, X 25. o outer integument. i inner integument. en fan shaped arrangement of endosperm cells. a disintegrating nucellar tissue.

Fig. 28. Section of another seed, same age as that of fig. 26, X 25. a nucellus. c radial arrangement of endosperm cells. d central cavity.

Fig. 29. Detail of a part of the same section as that of fig. 26, X 57. c micropylar region. o outer integument. i inner integument. a and b cells of outer integument filled with oily matter.

Fig. 30. Still finer detail of figure 26, X 290. a endosperm cells in the region of the embryo.

Fig. 31. Detail of the free nuclei and protoplasm as found at *b* fig. 24, X 425.

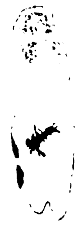
Fig. 32. Detail of nucellar tissue in chalazal region, as at *a* fig. 28, X 450. a cell walls, contents of cells having disappeared. b normal nucellus cells.

Fig. 33. Detail showing the condition in the chalazal region in many sections, X 425. b endosperm margin. a margin of disintegrating nucellus. c tissue consisting of free nuclei and protoplasm and lying between endosperm and nucellus.

Fig. 34. Detail of endosperm as seen at *e* fig. 28, X 425.

Fig. 35. Detail of cells of the outer integument and especially of the chalazal region that have oily deposits in them, X 425.

Fig. 36. Detail of one of the free nuclei of the endosperm as seen at *b* fig. 22, equatorial plate stage, X 1550.



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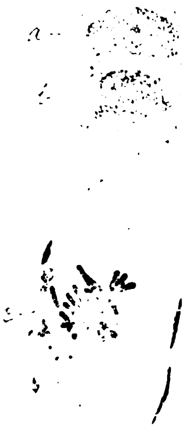

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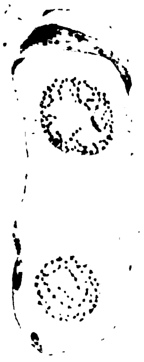

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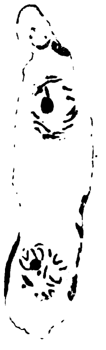

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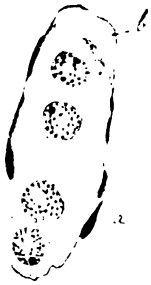

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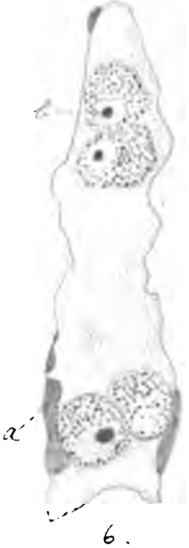

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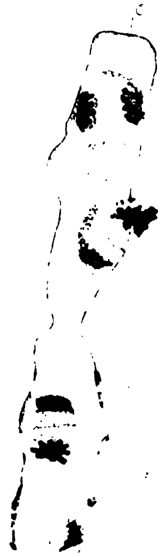

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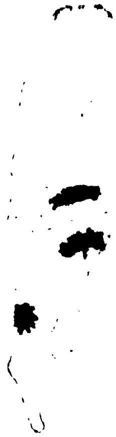

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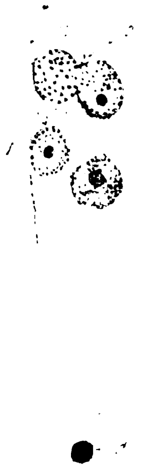

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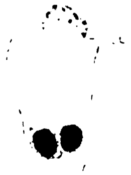

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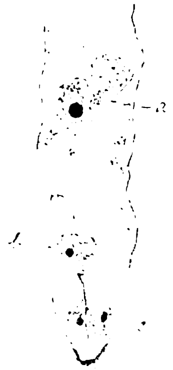

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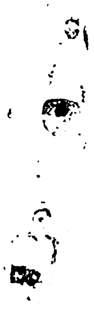

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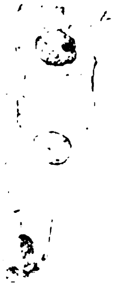

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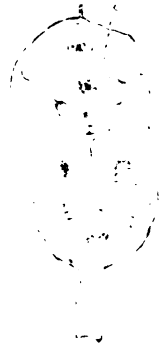

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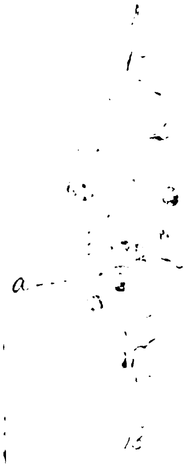

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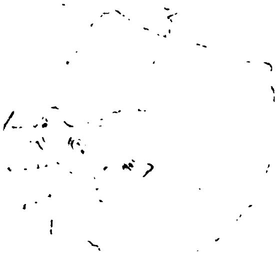

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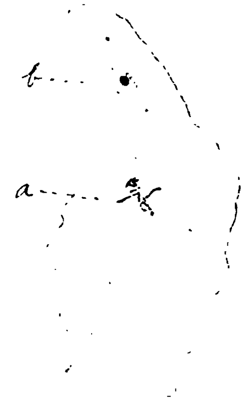

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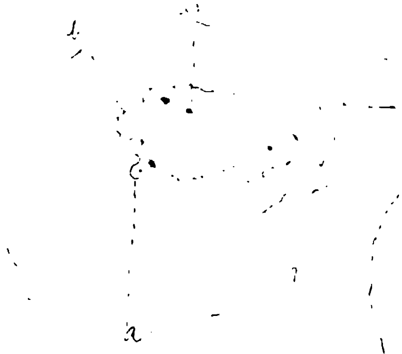

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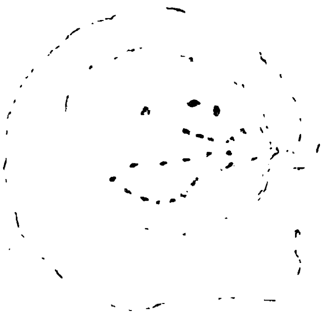

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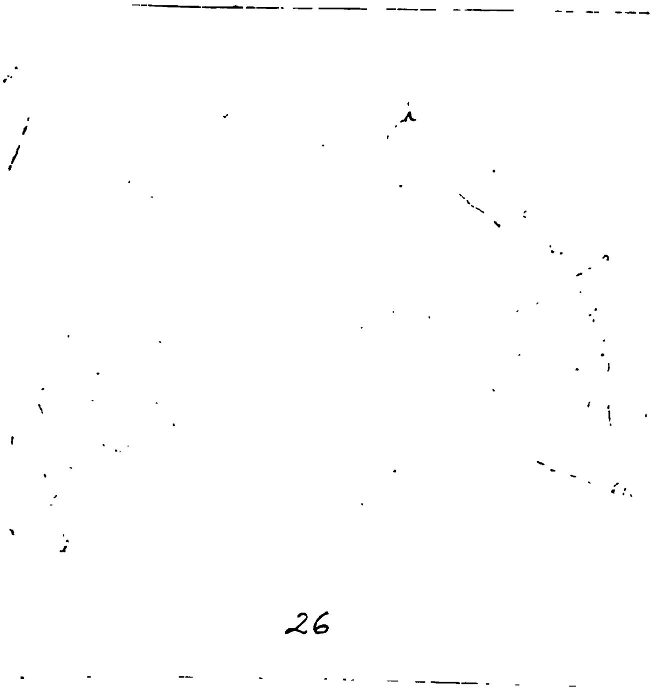

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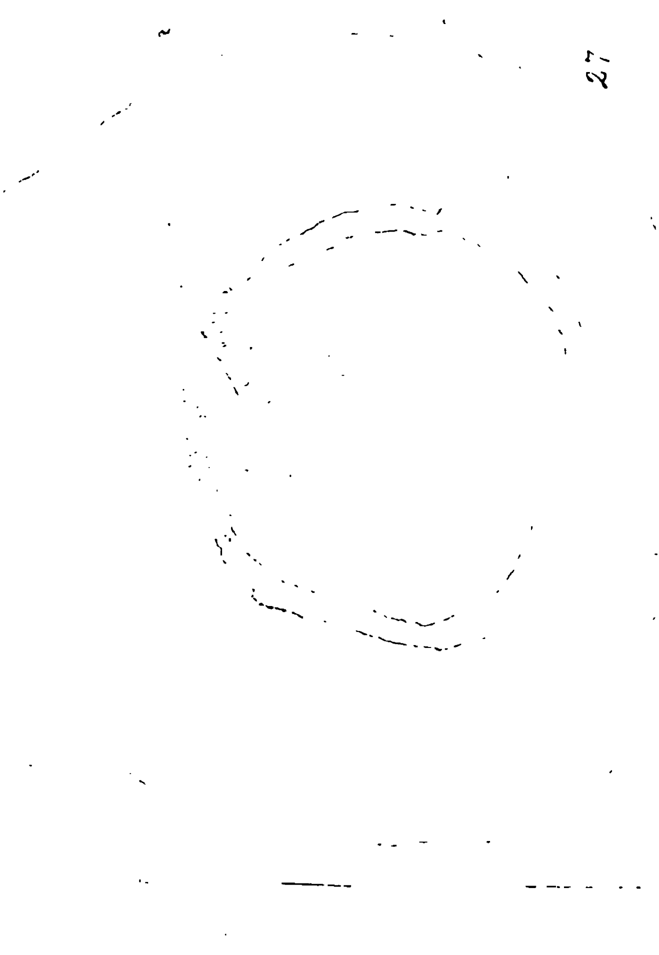

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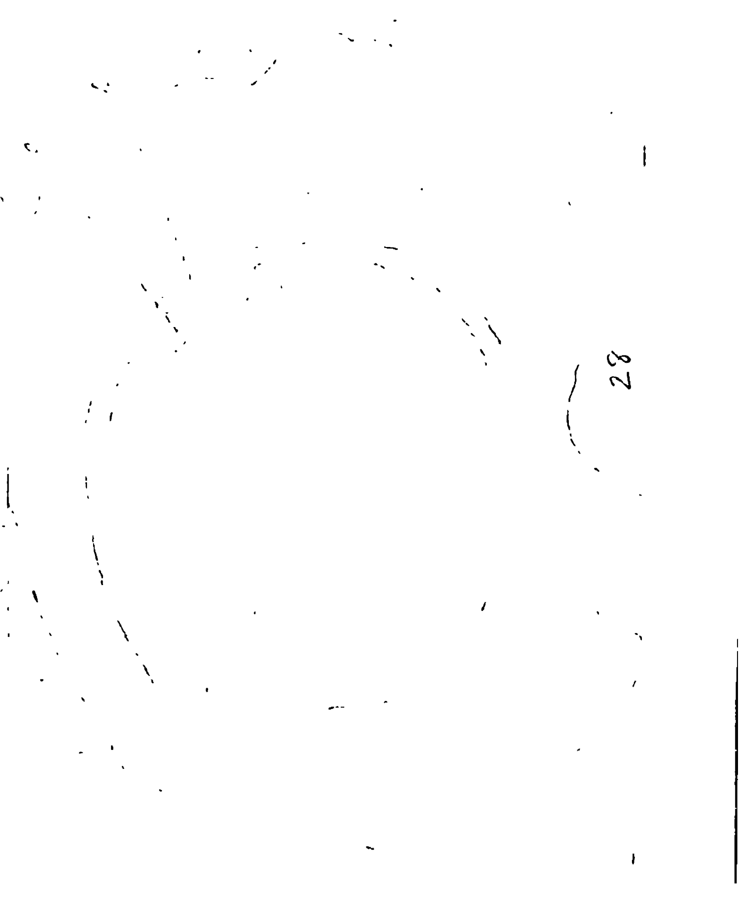

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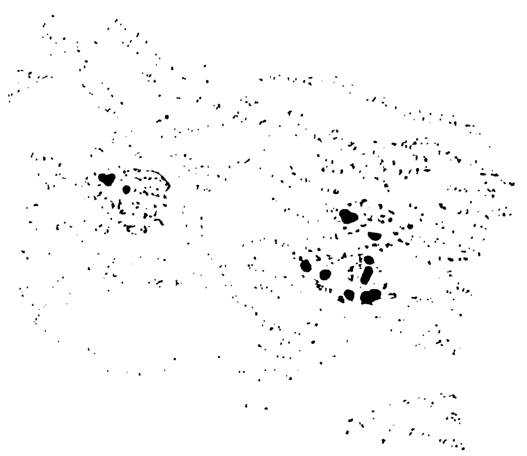

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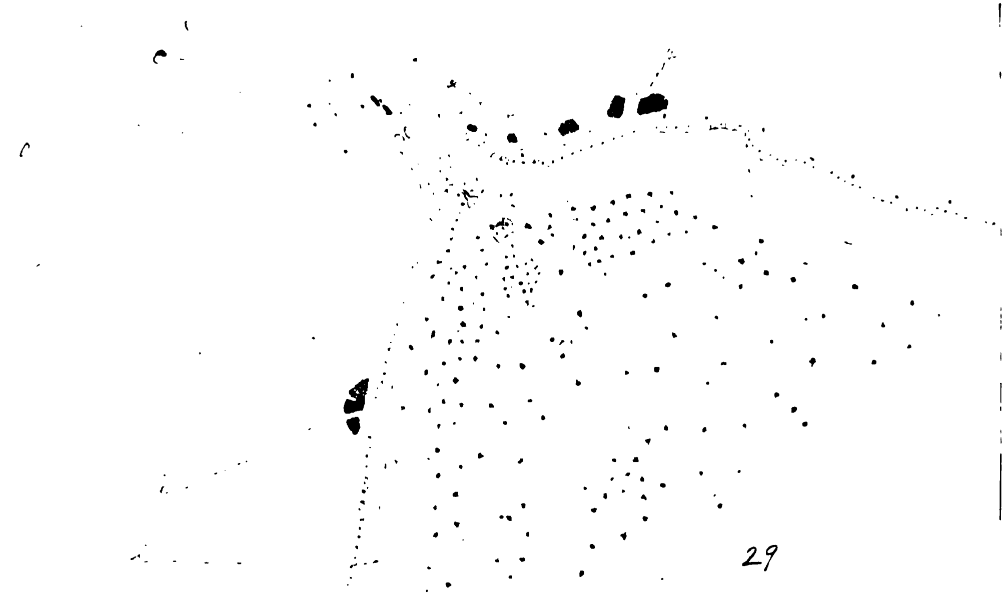

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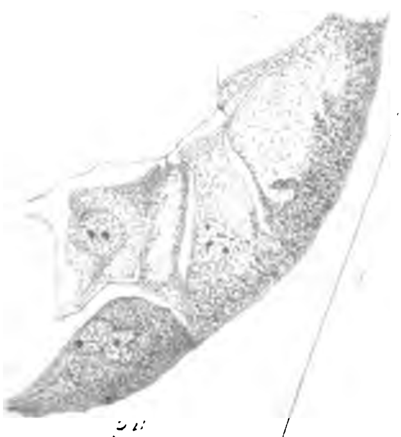

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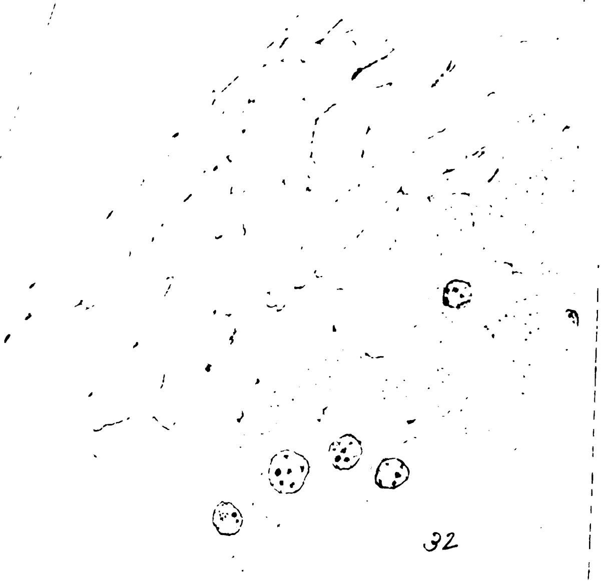

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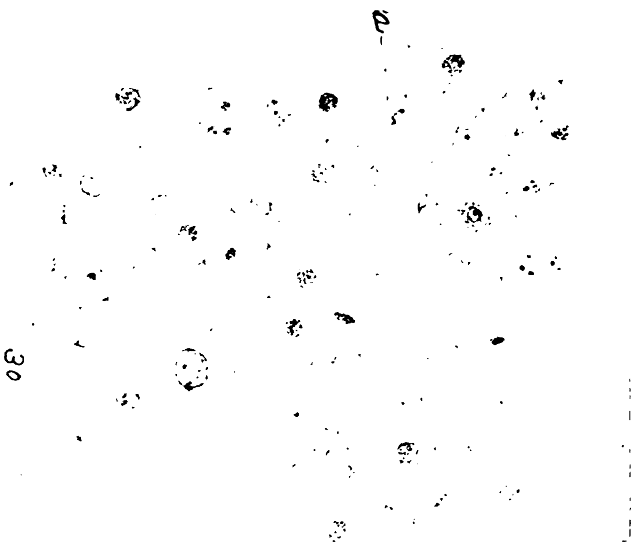

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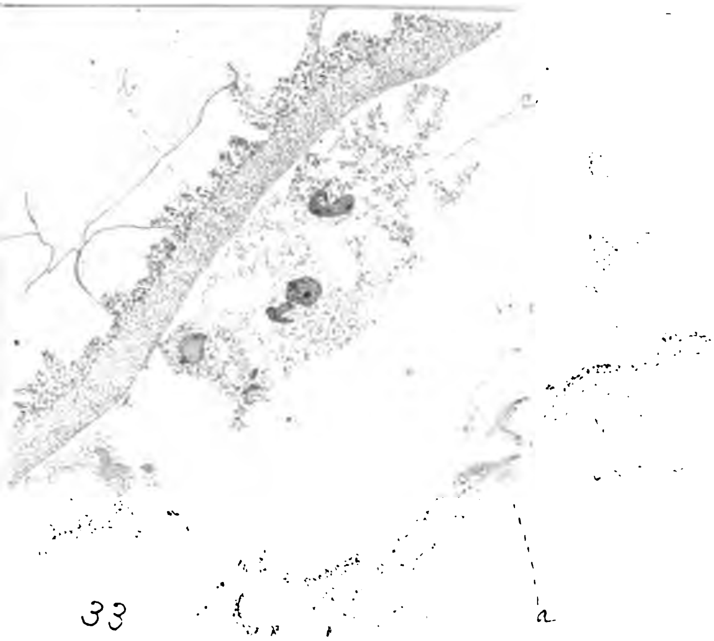

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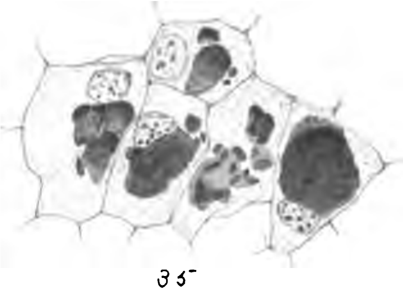

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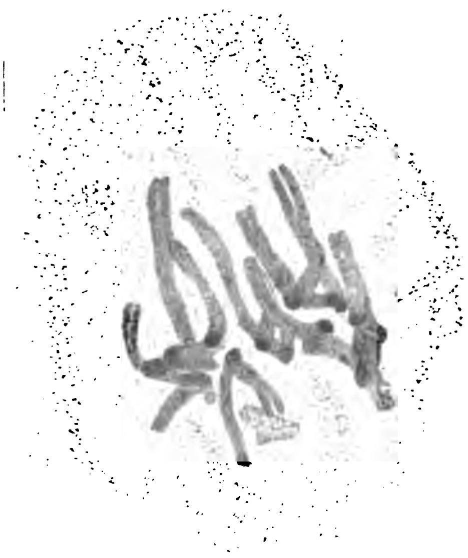

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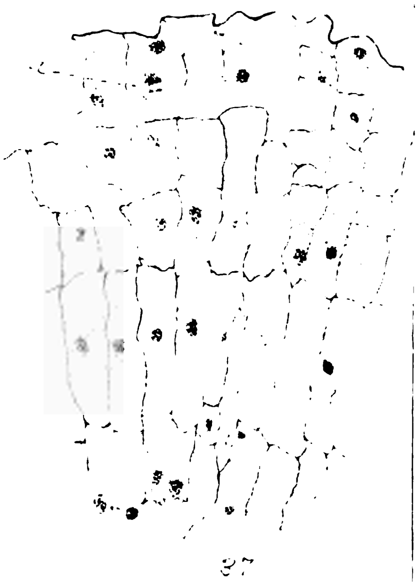

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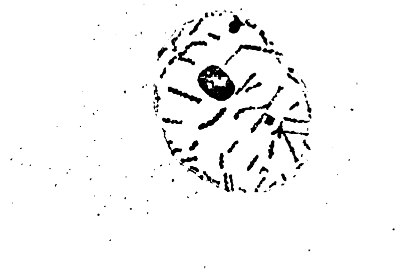

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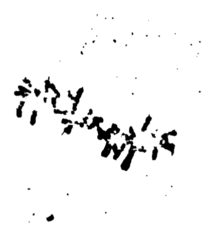

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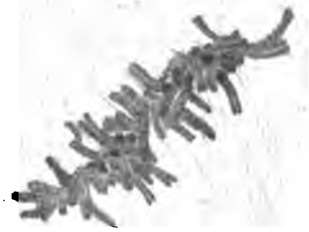

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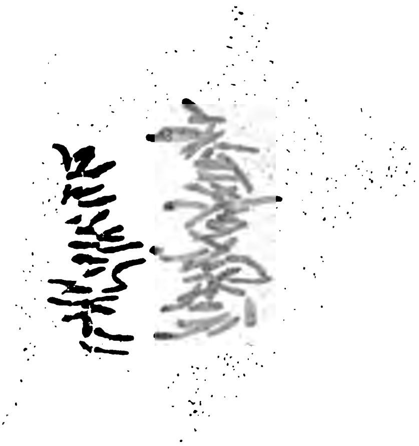

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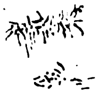

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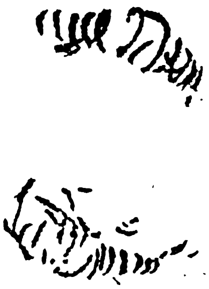

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Approved June 5

R A Harper

M. V. O'Shea

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